

1 Evolutionary Biology

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3 ESSAY

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5 **Homology: Homeostatic Property Cluster Kinds in Systematics and Evolution**

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7 **Leandro C.S. Assis • Ingo Brigandt**

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9 L. C. S. Assis (author for correspondence)

10 Laboratório de Sistemática Vegetal, Departamento de Botânica, Universidade de São

11 Paulo, Rua do Matão 277, São Paulo, SP, 05508-090, Brazil, Tel: 55 11 3091 7545,

12 Fax: 55 11 3091 7547

13 e-mail: lcsassis@ib.usp.br

14

15 I. Brigandt

16 Department of Philosophy, University of Alberta, 2-40 Assiniboia Hall, Edmonton AB

17 T6G 2E7, Canada, Tel: +1 780-492-0623, Fax: +1 780-492-9160

18 e-mail: brigandt@ualberta.ca

19 **Abstract** Taxa and homologues can in our view be construed both as kinds and as  
20 individuals. However, the conceptualization of taxa as natural kinds in the sense of  
21 homeostatic property cluster kinds has been criticized by some systematists, as it seems  
22 that even such kinds cannot evolve due to their being homeostatic. We reply by arguing  
23 that the treatment of transformational and taxic homologies, respectively, as dynamic  
24 and static aspects of the same homeostatic property cluster kind represents a good  
25 perspective for supporting the conceptualization of taxa as kinds. The focus on a  
26 phenomenon of homology based on causal processes (e.g., connectivity, activity-  
27 function, genetics, inheritance, and modularity) and implying relationship with  
28 modification yields a notion of natural kinds conforming to the phylogenetic-  
29 evolutionary framework. Nevertheless, homeostatic property cluster kinds in taxonomic  
30 and evolutionary practice must be rooted in the primacy of epistemological  
31 classification (homology as observational properties) over metaphysical generalization  
32 (series of transformation and common ancestry as unobservational processes). The  
33 perspective of individuating characters exclusively by historical-transformational  
34 independence instead of their developmental, structural, and functional independence  
35 fails to yield a sufficient practical interplay between theory and observation. Purely  
36 ontological and ostensional perspectives in evolution and phylogeny (e.g., an  
37 ideographic character concept and PhyloCode's 'individualism' of clades) may be  
38 pragmatically contested in the case of urgent issues in biodiversity research,  
39 conservation, and systematics.

40

41 **Keywords** Characters • Individuals • Monophyly • Natural kinds • Phylogeny •  
42 Similarity • Taxonomy • Transformational and taxic homology

## 43 **Introduction**

44

45 Taxa (hereafter, monophyletic groups) have been construed as *classes* (which have  
46 members and are not spatio-temporally continuous and cohesive entities embedded in  
47 the evolutionary contingency), or alternatively as *individuals* (which are wholes having  
48 parts and are spatio-temporally continuous and cohesive entities embedded in the  
49 evolutionary contingency; Rieppel, 2006). This seeming philosophical dichotomy  
50 between classes and individuals has generated renewed approaches and debates in  
51 contemporary systematics – theoretically, methodologically, and philosophically – such  
52 as the elaboration of an ideographic character concept (Grant and Kluge, 2004) and the  
53 clash between phylogenetic nomenclature and Linnaean taxonomy (Keller *et al.*, 2003;  
54 Nixon *et al.*, 2003; Pleijel and Härlin, 2004; Wheeler, 2004; Rieppel, 2006; Cantino and  
55 de Queiroz, 2007; and references therein).

56       However, this dichotomy is considered largely irrelevant for contemporary  
57 systematics by those arguing that taxa can be conceptualized as *homeostatic property*  
58 *cluster (HPC) kinds* (Keller *et al.*, 2003; Franz, 2005; Rieppel, 2005a, b, 2006, 2007a;  
59 Assis, 2009). Originally introduced by Richard Boyd (1991, 1999), the HPC construal  
60 of kinds attempts to reconcile the fact that kinds in the biological and social sciences are  
61 typically heterogeneous and cannot be defined by necessary or sufficient conditions  
62 (essences, which define classes), with the observation that such categories are not  
63 formed in an arbitrary fashion and epistemically permit scientific generalizations and  
64 explanations (Wilson *et al.*, 2009). The approach suggests that a kind is ontologically  
65 characterized by a *property cluster*, i.e., a larger set of properties that exhibit a relevant  
66 degree of correlation, where each kind member possesses several (though usually not

67 all) of these properties, and no single property must necessarily be shared by all kind  
68 members. Such a kind is a natural kind (rather than an arbitrary collection of objects) if  
69 the clustering of the various properties is due to underlying causal processes, so-called  
70 *homeostatic processes*.

71 In the context of phylogenetic systematics, the property cluster characterizing a taxon  
72 consists of taxic homologies or synapomorphies (Keller *et al.*, 2003; Franz, 2005;  
73 Rieppel, 2006). Common descent (involving reproduction across generations) is here  
74 the ‘homeostatic process’ that accounts for the clustering of these characters and the fact  
75 that phylogenetic classifications have a rich information content, e.g., “the  
76 characterizations of 38,000 kinds of spiders by their spinnerets (silk-producing glands),  
77 or of 250,000 kinds of flowering plants by their endosperm (resulting from the process  
78 of double fertilization)” (Franz, 2005, p. 497). Thus, homeostatic property cluster kinds  
79 are “scientific categories posited by our theories as epistemological devices; insofar as  
80 they have ontological status, it is as features of the ways in which causal structures in  
81 the world interact with our classificatory practices in such a way as to support reliable  
82 induction and explanation” (Keller *et al.*, 2003, p. 102). This thesis is claimed to allow  
83 natural kinds to be historically delimited, because of the reference to common ancestry  
84 in the case of taxa (Keller *et al.*, 2003; Rieppel, 2007a, b).

85 A few have suggested that there is no incompatibility between a taxon being  
86 construed both as a kind and as an individual (Dupré, 1999; LaPorte, 2004; Brigandt,  
87 2009), for both constructions are context sensitive. However, the conceptualization of  
88 taxa as natural kinds even in the sense of homeostatic property cluster kinds has been  
89 criticized by some systematists (e.g., Kluge, 2003; Grant and Kluge, 2004), as it seems  
90 that even such kinds cannot evolve due to their being based on homeostatic processes.

91 However, we reply by arguing that the treatment of transformational and taxic  
92 homologies, respectively, as dynamic and static aspects of the same homeostatic  
93 property cluster kind offers a good perspective for supporting the conceptualization of  
94 taxa as kinds. The focus on a phenomenon of homology (i.e., the relation of  
95 correspondence between parts of two or more organisms) based on causal processes  
96 (e.g., topology, connectivity, activity-function, ontogeny, genetics, inheritance, and  
97 modularity in development and evolution) and implying relationship with modification  
98 yields a notion of natural kinds conforming to the phylogenetic-evolutionary  
99 framework.

100 While assuming that ontologically speaking an individual and a kinds approach are  
101 consistent, we focus on articulating how to construe taxa and in particular homologues  
102 as HPC kinds, because some still argue that this is impossible, and – more importantly –  
103 because we explore new perspectives, showing how the HPC approach motivates and  
104 successfully addresses them. This paper recommends the notion of HPC kinds for its  
105 heuristic and theoretical fruitfulness in tying taxic to transformational homology,  
106 combining empirical-pragmatic and theoretical-explanatory aims in taxonomy and  
107 evolutionary biology, and making accounts of homology germane to a plethora of  
108 issues. This embraces evolvability, adaptation, diversification, research on the  
109 developmental-functional make-up of organisms, the phylogeny-taxonomy link,  
110 biodiversity and conservation policies, as well as the continuity of philosophy with  
111 empirical science. We do not maintain that the individuals perspective is wrong, but  
112 challenge it on the grounds that it has not previously motivated the indispensable issues  
113 in systematics and evolution we explore in these pages.

114

115 **From properties of classification to events of generalization**

116

117 Some metaphysically realist systematists influenced by the purely ontological  
118 conception of species and monophyletic groups as individuals such as Grant and Kluge  
119 (2004, p. 25) have criticized the construal of character states as properties: “character-  
120 states have generally been conceptualized as properties (attributes, features), which  
121 logically denies their ability to transform or evolve, since properties are class concepts  
122 and, as such, immutable.” Instead they propose an ideographic character concept: “as  
123 transformation series, characters are historical individuals akin to species and clades”  
124 (Grant and Kluge, 2004, p. 23). Accordingly, character states are “*the least inclusive*  
125 *historical individuals that result from heritable transformational events*” (Grant and  
126 Kluge, 2004, p. 26; emphasis in original). And “because the basic or fundamental unit  
127 in phylogenetic inference is the transformation event, the relevant independent parts of  
128 organisms are those that have undergone independent, heritable transformation events.  
129 What matters in individuating character-states (and more inclusive transformation  
130 series), therefore, is not the structural, developmental, or functional independence of a  
131 part, but its historical/transformational independence” (Grant and Kluge, 2004, p. 26;  
132 contra Rieppel and Kearney, 2002). Hence, a strict ontological character concept is  
133 proposed that represents the primacy of generalization (e.g., an explanatory theory of  
134 historical singular processes) over classification (e.g., contextual patterns of  
135 membership relations by properties) in phylogenetic systematics (cf. Rieppel, 2004).  
136 Correspondingly, Grant and Kluge (2004, p. 25) reject the possibility of construing  
137 species as kinds, even as homeostatic property cluster kinds, claiming that “in being  
138 homeostatic, such kinds cannot evolve.”

139        However, when assuming that a character, as a relation of ‘sameness’ captures the  
140        notion of transformational (e.g., the homologues A and A’) and taxic homologies (e.g.,  
141        A’), the tenet of Kluge (2003) and Grant and Kluge (2004) about the non-phylogenetic-  
142        evolutionary nature of HPC kinds fails to meet its target, because a hypothesis of  
143        transformational and taxic homologies – as we will see below – are critical for making  
144        the idea that homologies and taxa are HPC kinds conform to an evolutionary  
145        framework. An important point is that the fundamentals of transformational and taxic  
146        homologies in phylogenetic theory and practice are not strictly ontological like an  
147        ideographic character concept is. They are also epistemological and, as such, instantiate  
148        a relation of classification (or knowledge of observational facts) to generalization (or  
149        explanatory theories of unobservable phenomena). In fact, conjectures of  
150        transformational and taxic homologies are firstly established by the empirical-  
151        contextual delineation of characters (i.e., by similarity or correspondence) with their  
152        subsequent polarization (i.e., definition of relatively correspondent plesiomorphic and  
153        apomorphic character states within characters onto the phylogenetic hierarchy; Bryant,  
154        2001) by cladogram rooting (see Grant *et al.*, 2006, as an example of these empirical  
155        and logical approaches). And only after the hierarchical construction the evolutionary  
156        explanation is carried out. It is in this way that the conceptualization of taxa as HPC  
157        natural kinds and their accommodation to evolutionary properties and events (contra  
158        Grant and Kluge, 2004) must be further investigated through the treatment of  
159        transformational and taxic homologies as dynamic and static aspects of a homology, and  
160        thus as different aspects of the same HPC kind, which thereby permits phylogenetic  
161        relatedness and modification.

162

163 **Transformational and taxic homologies, modification and homeostasis**

164

165 It turns out to be erroneous to assume (as Kluge, 2003 and Grant and Kluge, 2004 do)  
166 that an entity whose identity is based on homeostatic processes – at least as this notion  
167 is used in the HPC construal of kinds – is essentially unchanging in most of its features.  
168 Rieppel (2005a, p. 482) discusses the meaning of homeostasis as “the maintenance of a  
169 dynamically stable internal environment in an open system.” In this way, an individual  
170 organism is a dynamically stable system that keeps many properties during its life time,  
171 despite undergoing ontogenetic development as change in other properties (e.g., its  
172 series of semaphoronts; see Hennig, 1966). There are ‘homeostatic’ processes that  
173 explain both why the individual keeps its identity across time and can change as an  
174 integrated entity, including self-maintenance as a variety of cellular, physiological, and  
175 behavioral processes (Wagner and Laubichler, 2001), phenotypic plasticity and  
176 developmental constraints (Rieppel, 2005a, b).

177 The same idea applies to a species taxon construed as an HPC kind (Wilson *et al.*,  
178 2009). Conspecifics share many features in certain combinations – the cluster of  
179 properties characterizing an HPC kind. This correlation and distribution of properties is  
180 explained by processes accounting for species cohesion, as laid out by different species  
181 concepts. One such process is gene flow. Gene flow across conspecifics is not at all  
182 incompatible with evolutionary change; in fact, it accounts for why a species changes *as*  
183 *a coherent unit*, should it change due to natural selection and other influences, since  
184 change in some populations is transmitted via gene flow to the rest of the species. Thus,  
185 the so-called ‘homeostatic’ processes account for why the members of an HPC kind  
186 existing at the same point in time exhibit similarities, and why change typically affects

187 all kind members, so that the kind changes as a unit. Gene flow and the ability to  
188 interbreed are relational rather than intrinsic properties, but the HPC approach permits  
189 such properties and considers them as important for the identity of biological kinds,  
190 including the relational property of common descent.

191 This brings us to the ability of characters to evolve, as emphasized by Grant and  
192 Kluge (2004). An important issue for construing characters as HPC kinds consistent  
193 with an evolutionary framework is the relation between ontogeny, inheritance, and  
194 phylogeny, where the concepts of homologue and homology as well as semaphoront  
195 and ‘complex semaphoront’ are fundamental. A homologue is “a part of an organism”  
196 and homology is “a phylogenetic relationship between parts, or homologues of different  
197 organisms” (Nelson, 1994, p. 104). According to Hennig (1966, p. 65), “the  
198 semaphoront corresponds to the individual in a certain, theoretically infinitely small,  
199 time span of its life, during which it can be considered unchangeable,” whereas “a  
200 ‘semaphoront complex’ can be constructed by aspect fusion of several aspect continua  
201 representing the same organism at different ontogenetic stages” (Rieppel, 2003, p. 172).  
202 As an organism is contextually composed of parts (homologues), each such part,  
203 throughout its ontogenetic stages, is characterized by a complex semaphoront.  
204 Developmental and genetic constraints act in the construction of the ‘semaphoront  
205 complex’ as a dynamic entity integrated by homeostatic processes, so that each one of  
206 its semaphoronts corresponds to a static, ‘unchangeable’ stage in a certain time span of  
207 the organism’s life. “But just as a ‘semaphoront complex’ [i.e., an ontogenetic unity]  
208 can be constructed for a single organism, so it can also be constructed by aspect fusion  
209 for species and higher taxa” (Rieppel, 2003, p. 172). As such, taxa can be  
210 conceptualized as “phylogenetic relationships [...] of ontogenetic parts of life” (Nelson,

211 1989a, p. 279), so that these parts are homologues (e.g., A or A') of a character in  
212 different organisms, and these homologues, in the phylogenetic-evolutionary hierarchy,  
213 capture relations of transformational and taxic homologies.

214 The *transformational* perspective on homology, i.e., the relation between different  
215 states of a character found in two or more organisms, is concerned with change (e.g.,  
216  $A \rightarrow A'$ ) and need not imply grouping (Patterson, 1982; Rieppel, 1988). The *taxic*  
217 perspective, i.e., the relation between identical, apomorphic character states shared by  
218 two or more organisms, is concerned with common ancestry and grouping (e.g., A'),  
219 being operationally established by the overall congruence of characters in a hierarchy  
220 (Patterson, 1982) (i.e., a set-theoretical notion irrespective of causal phenomena, unless  
221 it is qualified by causal-contextual efficacious properties; Rieppel, 2004). The  
222 transformational account with its focus on evolutionary change represents the *dynamic*  
223 aspect of the HPC kind (i.e., a phenomenon of homology), whereas the taxic account  
224 with its relation to the monophyly and classification of groups represents the *static*  
225 aspect of the same HPC kind.

226 This is possible as there are different properties ontologically associated with an  
227 HPC kind, some of which are more static, while others are more dynamic. Some of  
228 these properties are causally more basic, while others are the effects of the former; some  
229 are non-observational, while others are observable (Brigandt, 2009). In the case of a  
230 higher taxon as an HPC kind, descent from a particular ancestral species is a (non-  
231 observational) causally basic feature that *explains* why the (observable) apomorphies of  
232 the taxa members – some further properties of the HPC cluster – are shared, and  
233 common ancestry is a property shared by taxa members that permits other properties  
234 (characters) to change and evolve. A species taxon construed as an HPC kind is

235 ontologically characterized by many features that stand in complex and reciprocal  
236 causal relations, e.g., genetic properties of individuals, their phenotypic features, gene  
237 flow and the ability to interbreed, ecological competition, and developmental  
238 constraints (Wilson *et al.*, 2009). Rieppel (2008) emphasizes that a particular scientific  
239 approach is typically interested in only certain aspects tied to a kind, be it phylogenetic,  
240 developmental, functional, anatomical, or ecological features. Indeed, there are different  
241 species concepts based on different biological features and operational approaches (see  
242 Wheeler and Meier, 2000; and references therein). Yet the fact that only some features  
243 of a taxon or a homology are of epistemological or pragmatic interest in a certain  
244 scientific context does not entail that there are no other features ontologically tied to this  
245 entity that may be relevant given other scientific interests; and the HPC approach  
246 explains how different perspectives on a kind can be consistent and related.

247       In the case of a homology (a character across generations) as an HPC kind, certain  
248 genetic-developmental properties of the character permit that it can be inherited across  
249 generations and undergo change of state while remaining the same morphological unit  
250 (Wagner, 1996, 2001; Jamniczky, 2008). Wagner (2007) presents evidence that the  
251 identity of a character is established by *certain* gene regulatory networks, which have  
252 been stable across evolutionary change (so that the character is present in several extant  
253 species), while *other* genes have evolved leading to this character taking different states  
254 in ancestral and extant species. This illustrates how different features are tied to an HPC  
255 kind – some of which are more evolutionary stable, some of which are subject to change  
256 – and that a character construed as an HPC kind can evolve (contra Grant and Kluge,  
257 2004).

258       Grant and Kluge (2004) restrict the notion of homology to the transformational

259 account. But by regarding homology as both a homeostatic property cluster kind and a  
260 relation between parts, we conceive homology within a broader scope. In this manner,  
261 the same phenomenon of homology (as an HPC kind) encompasses the *transformative-*  
262 *dynamic* aspect of homologues (e.g.,  $A \rightarrow A'$ ) and the *taxic-static* aspect of one such  
263 homologue or character state (e.g.,  $A'$ ) shared ontologically by all descendants and their  
264 most recent common ancestry. Monophyly integrated with developmental and genetic  
265 constraints are the homeostatic processes that determine a taxon's boundary (Brigandt,  
266 2009). As taxic homologies are responsible for the identification and classification of  
267 monophyletic groups, their importance over transformational homologies has been  
268 pragmatically endorsed in phylogenetic theory and practice (see Patterson, 1982;  
269 Rieppel, 1988; de Pinna, 1991; Brower and Schawaroch, 1996). Criticisms have been  
270 made regarding the ontological nature of a transformation series (see Rieppel, 1988).  
271 But whereas most of the papers concerned with the integration of the theory of natural  
272 kinds and phylogenetic systematics focus on the treatment of taxic homologies (or  
273 synapomorphies) as HPC kinds (e.g., Keller *et al.*, 2003; Franz, 2005; Rieppel, 2005a,  
274 b, 2006), transformational homologies – the most critical feature to dispel the idea that  
275 an HPC kind cannot evolve – have only recently been considered (see Brigandt, 2007,  
276 2009).

277       Since a taxic homology, i.e., the apomorphic homologue that identifies a  
278 phylogenetic relationship as a taxon, is included in a series of transformations, it is an  
279 ongoing phenomenon in the world (Keller *et al.*, 2003). As such, it is subject to  
280 modification. Moreover, by regarding the causal-contextual properties (or tokens) that  
281 define a taxon (qua natural kind) as embedded in the evolutionary contingency, one has  
282 to expect the occurrence of some reversions (i.e., the appearance of an apomorphic

283 condition within a natural kind, so that this condition is similar to the plesiomorphic  
284 condition found at a more inclusive level in which that natural kind is contained) and  
285 derivations (new character states). Other homologues (as HPC kinds) found in the taxon  
286 are also subject to change and consequently promote diversification and novelty within  
287 it. For instance, in the phylogeny of Reptilia, the position of turtles (Testudines,  
288 classically considered anapsids) within Diapsida reveals that the lack of holes behind  
289 the eye socket is – following the phylogenetic levels of universality – a reversion in  
290 Reptilia, an apomorphic or derivate condition in Diapsida (which is phylogenetically  
291 circumscribed by the presence of two holes behind the eye socket), and a synapomorphy  
292 of Testudines (see Rieppel, 1999; and references therein). In this way, lack and presence  
293 of holes behind the eye socket are states that characterize the skull of Diapsida and  
294 Reptilia as a causal, historical, and dynamic unit integrated by homeostatic processes,  
295 which is related to certain events of origin and diversification within these groups.

296 Since the notion of homologies as HPC kinds embraces relationship with  
297 modification, it is germane to evolvability, “the capacity of a developmental system to  
298 evolve” (Hendrikse *et al.*, 2007, p. 394). In other words, evolvability “is a disposition  
299 that an organism and its homologues can possess” (Brigandt, 2007, p. 712). In line with  
300 this, morphological organization into distinct homologues, developmental constraints,  
301 and modularity explain evolvability (Yang, 2001; Brigandt, 2007; Jamniczky, 2008).  
302 This perspective plus the theory of HPC kinds can also be used in studies of  
303 diversification, selection, and adaptation (e.g., Yang, 2001). According to Brigandt  
304 (2007), in contrast to what has often been assumed, developmental constraints and  
305 selection are not antagonistic forces, but complementary. For developmental constraints  
306 are related to the developmental generation and evolutionary maintenance of

307 homologues as units of morphological variation across generations (identity of a  
308 morphological unit despite its phenotypic change), while natural selection subsequently  
309 operates on the produced variation (resulting in character transformation).

310 In fact, Yang (2001) argues that developmental aspects of juveniles and adults stages  
311 of hemi- and holometabolous insects can be conceived of as modules (or causal  
312 properties) of evolutionary change relative to events of diversification and adaptation.  
313 The author highlights that, based on these features, Holometabola was found to have a  
314 significant rate of diversification when compared to its sister-group Eumetabola  
315 (traditionally a hemimetabolous). In addition, Yang (2001) shows that the characters in  
316 more modular monophyletic groups partake in greater levels of variation due to their  
317 independence. This may imply that developmental constraints and selection act  
318 complementarily in the static and dynamic aspects of these insects' parts or modules  
319 (i.e., homologues as a HPC kinds), and consequently, in their events of origin and  
320 diversification.

321

### 322 **Similarity again and forever**

323

324 Identical or similar character states in a monophyletic group are *one* aspect of an HPC  
325 kind. However, Ereshefsky (2007, p. 296) charges that "HPC's emphasis on similarity  
326 is at odds with phylogenetic approaches to taxonomy." We reply by pointing out that  
327 apart from members of the same HPC kind sharing certain internal features, there are  
328 also *relations to members of other kinds*, which in this case account for a character (a  
329 homology) being a unit of evolutionary transformation. Some of the genetic-  
330 developmental properties of a morphological structure (or developmental module)

331 pertain to how this structure is partially developmentally dissociated from other  
332 structures, so that across generations it can vary and evolve largely independently of  
333 other structures (Brigandt, 2009). Among other things, the growing literature on  
334 modularity works towards an explanation of how structures that exhibit some  
335 developmental and functional relations can be sufficiently dissociated so as to permit  
336 morphological change (von Dassow and Munro, 1999; Schlosser and Wagner, 2004;  
337 Rieppel, 2005b). What makes a character a phylogenetic unit is its ability to evolve  
338 independently of other characters (Wagner and Laubichler, 2001). Construing a  
339 character as an HPC kind is not only consistent with a character being able to evolve,  
340 but some of the developmental relations and dissociations w.r.t. other characters – an  
341 aspect of the HPC kind in addition to internal similarities – explain this ability to evolve  
342 in a character-by-character fashion (Brigandt, 2007).

343 To be sure, the relations of correspondence among different character states (i.e.,  
344 transformational homology as a dynamic aspect of an HPC unit) and the same  
345 homologues (i.e., taxic homology as a static aspect of an HPC unit) are causally and  
346 contextually evidenced according to heterogeneous criteria of comparative biology, as a  
347 way of seeing the biological world whereby similarity / correspondence between parts  
348 of organisms (homologues) is empirically and theoretically justified by activity-  
349 function, ontogeny, genetics, inheritance, and modularity in development and evolution.  
350 Yet it is important to bear in mind that these developmental, functional, and modular  
351 phenomena are largely unexplored for characters in phylogenetic inferences, and that  
352 these relations need to be established by classical approaches to comparative biology,  
353 such as topological relations and/or connectivity (the resemblance in position and  
354 arrangement between structures) (Rieppel, 1988; Rieppel and Kearney, 2002; Kearney

355 and Rieppel, 2006). These two classical criteria of correspondence are conventionally  
356 and more or less successfully used throughout the systematic and comparative endeavor  
357 as the panacea for solving problems of the common origin of homologues (Rieppel and  
358 Kearney, 2002; Kearney and Rieppel, 2006). Indeed, as monophyly is not immediately  
359 given, it must be parasitic on homology (see Dupré, 1981; Nelson, 1994; Rieppel, 2003,  
360 2006). Taxa and characters delineation is empirical-contextual (Franz, 2005).

361       Following the thesis of individualism, Grant & Kluge (2004) stress that  
362 developmental independence is not fundamental for individuating historical character-  
363 states in phylogenetic systematics, whereas Ghiselin (2005) realizes that homologies as  
364 historical entities / individuals are grounded among other things in developmental  
365 processes. In the context of an empirical-contextual discourse, homologies and taxa as  
366 individuals are levels of biological organization with asymmetric construction.  
367 Homologies can be construed by substantial knowledge (see Ghiselin, 2005), but taxa  
368 cannot. Specific parts or processes (e.g., developmental and taxic homologies) do not  
369 define taxa as individuals, for these are whole-part relations. Hence, the individualism  
370 of taxa cannot be grounded in data matrix and cladogram construction (contra Cantino  
371 and de Queiroz, 2007; Ereshefsky, 2007). The only way of making reference to their  
372 individualistic monophyly is by stipulation plus ostensional indication (i.e., by ‘pointing  
373 out’ paradigmatic exemplars of a taxon without any empirical-contextual knowledge  
374 about its referent; cf. Rieppel, 2007b, 2008). Accordingly, the perspective of  
375 individuating characters exclusively by historical-transformational independence  
376 instead of a part’s developmental, structural, and functional independence (e.g., Grant  
377 and Kluge, 2004) is, in the language of systematics, virtually devoid of any practical  
378 interplay between theory and observation.

379

380

381 **Conclusions**

382

383 Taxa and homologues can in our view be construed both as kinds and as individuals  
384 depending on the context of a certain scope of discourse. Consequently, both  
385 constructions face the problem of instantiating theoretical-causal entities and the terms  
386 that name them w.r.t. two indispensable and reciprocal approaches – the  
387 epistemological knowledge of systematics and the metaphysical phenomenon of  
388 evolution. A successful perspective for making the theory of homeostatic property  
389 cluster kinds conform to phylogenetic systematics depends upon the treatment of  
390 transformational and taxic homologies, respectively, as dynamic and static aspects of  
391 the same phenomenon of homology (i.e., as modification and relationship in a  
392 hierarchical reconstruction) grounded in efficacious causal-contextual properties. These  
393 properties capture relations of similarity (in language by predicates; Rieppel, 2007b),  
394 which are fundamental for phylogenetic reconstructions, classifications of biodiversity,  
395 and related approaches (Assis, 2009). The transformational account of homology  
396 focuses on how a character is inherited and gradually modified through generations and  
397 species, while the taxic approach focuses on a split in a lineage (formation of different  
398 taxa) and the resulting marked differences between extant species of different taxa.

399 An adequate notion of HPC kinds establishes an epistemological and ontological  
400 basis for the naturalization of the Linnaean taxonomy – as a verbal reference system for  
401 systematics – grounded in Hennigian phylogenetic systematics – as a general reference  
402 system for systematics (Hennig, 1966) –, and the consequent replacement of

403 paraphyletic groups or nominal kinds by monophyletic groups or natural kinds (Rieppel,  
404 2006). Nevertheless, the conceptualization of taxa as classes, in Linnaean taxonomy,  
405 and individuals, in Hennigian phylogenetics, can fruitfully be replaced by a construal of  
406 taxa as natural kinds (Keller *et al.*, 2003; Rieppel, 2006). For in addition to theoretical-  
407 explanatory aims HPC natural kinds satisfy simultaneously historical, empirical, and  
408 methodological demands of contemporary systematics. Thus, we recommend the HPC  
409 approach because of its heuristic fruitfulness for a variety of issues, not because it  
410 would metaphysically exclude the individualism approach.

411 Even though species and higher taxa are pragmatically and contextually  
412 circumscribed in different ways (i.e., there are different species concepts, and higher  
413 taxa are phylogenetically delimited by synapomorphies distributed in a cladogram),  
414 their ontological status in the systematics-evolution link is the same – they can be  
415 construed as HPC natural kinds. Therefore, it is false to assume an empirical difference  
416 between species and higher taxa as units of systematics and evolution (see Nelson,  
417 1989b). Both are contextually delineated based on (relational) properties and  
418 homeostatic processes at distinct levels of universality.

419 Historically, extensional and intensional definitions – empirically based accounts of  
420 characters, homologues, and taxa – when compared to an ostensional individuation or  
421 baptism (cf. Rieppel, 2007b), have provided great conceptual advances in our  
422 epistemological and ontological schemata in the context of systematics and the  
423 evolution of biodiversity. Substantial knowledge is consequently required for  
424 homologies' construal both as kinds and as individuals. In contrast, Grant and Kluge's  
425 (2004) metaphysical realism about individuals and characters does not provide an  
426 advancement in our knowledge of observational beliefs, concepts and terms relative to

427 the language of systematics and everyday life. At the end of the day, their ideographic  
428 character concept has merely ontological status that fails to do justice to the essential  
429 continuity of philosophy with empirical science.

430 As homeostatic property cluster kinds in systematics, evolution, and biodiversity  
431 research are fundamentally and historically rooted in the epistemological primacy of  
432 classification (e.g., homology and taxonomic hierarchy) over generalization (e.g., series  
433 of transformation and common ancestry) (see Rieppel, 2004), it emerges as an  
434 appropriate approach in an attempt to provide that continuity. As a result, a purely  
435 ontological assumption, stipulation, and ostension in evolution and phylogeny, e.g., the  
436 ideographic character concept (Grant and Kluge, 2004) and the ‘individualism’ of  
437 clades as endorsed by the PhyloCode (Cantino and de Queiroz, 2007; see also  
438 Ereshefsky, 2007), may be pragmatically contested in the case of urgent issues in  
439 contemporary systematics. These include the renaissance of taxonomy and comparative  
440 morphology, homology assessment, as well as the crisis, knowledge (e.g., faunas, floras,  
441 monographs, and revisions), phylogenetic classification, and the conservation of  
442 biodiversity (Wheeler, 2004; de Carvalho *et al.*, 2008; Assis, 2009).

443

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445

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452

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